Further development of the newborn *C. jacchus* and child transport by family members will be described elsewhere (ROTHE and DRENHAUS, in prep.).

Conclusions

The results referred to in this paper allow for a more or less full answer to our introductory questions. However, we have to keep in mind that further observations are necessary for a better understanding and interpretation of the delivery behaviour of the common marmoset.

1. The pregnant females withdraw from their family members about one hour before the onset of the dilatation period. None of the group members follows the female, nor do they — as long as the housing room is kept dark — pay any attention to it. Even vocalization of the labouring female and the smell of amnion fluid do not provoke the approach of any member of the family. The females gave birth to their offspring without any help from their group members, and they did not return into the common sleeping box after parturition. In our previous paper we have interpreted this behaviour, in accordance with BOWDEN et al. (1967) *(S. sciureus)*, as a protective reaction of the female against obtrusive group members who could endanger the mother and the neonates (consider for example the tearing of the umbilical cords by other animals when grasping the placenta). Our present data strongly suggest that the presence of other family members seems to be caused by an inadequate observation method (by full light).

2. Again it was difficult to determine the beginning and the end of the dilatation period. But the postures described above ("defecation" — and squatting-posture) of the females seem to us to be rather good criteria for the establishment of the dilatation period. However, further observations will have to prove or disprove this assumption.

3. The mother does not pay attention to the umbilical cord before the expulsion, viz. eating of the placenta. With undisturbed parturition (e. g. no observation by turned on lights) the mother is considered to always eat the placenta by herself.

4. Group members show great curiosity in the babies, on noticing them for the first time.

5. Again it became obvious that the mother's care for her young is limited to licking; she offers no help during the infant's way to her nipples shortly after expulsion. Therefore, weakly born infants do not have a fair chance to survive.

Summary

One single and one triple birth by two pluriparous *Callithrix jacchus* females living in family groups are described. Both deliveries took place at night between 19h00 and 22h30 and 01h00 and 04h00 respectively. The housing rooms were kept dark until the end of the parturition in the first case, and, in the second, until the beginning of the expulsion period. About one hour before the onset of the dilatation period, the pregnant females left the common sleeping box unnoticed by their group members. One female was alone during the whole delivery; her group members did not notice the baby before the morning (06h00). With the other delivery, the family members approached the mother after we had switched on the lights at the beginning of the expulsion period. They showed great interest in the babies but did not actually interfere with the delivery. Three infants were presented in vertex position, two of them in occiput posterior, one in occiput anterior. The last-born triplet was presented in breech position. The mother and other group members did not show much concern with the weakest born baby. With exception of this one presented in breech position, all other babies grasped the mother's fur immediately after their expulsion and reached the nipples without help. One female ate the placenta including the umbilical cord herself, the second at first paid no attention to the placenta which was then seized and eaten by other family members.

Zusammenfassung

Weitere Beobachtungen zum Geburtsverhalten des Weißbüscheläffchens (Callithrix jacchus)

Eine Einlings- und eine Drillingsgeburt zweier im Familienverband lebender pluriparer *Callithrix jacchus* ♀♀ werden beschrieben. Beide Geburten fanden während der Nacht zwischen 19h00 und 22h30 bzw. zwischen 01h00 und 04h00 statt. Solange die Beobachtungsräume nicht beleuchtet waren, wurde das gebärende ♀ bzw. die Neugeborenen von den übrigen Gruppenmitgliedern nicht bemerkt. Ungefähr eine Stunde vor dem Beginn der Eröffnungsphase sonderten sich die beiden ♀♀ von der Gruppe ab. Sie verließen den Schlafkasten, ohne von anderen Gruppenmitgliedern bemerkt zu werden. Ein ♀ war während der gesamten Geburt allein. Die Gruppe bemerkte das Neugeborene erst am Morgen. Dem anderen ♀ näherten sich die Familienmitglieder erst, nachdem wir die Raumbeleuchtung eingeschaltet hatten. Sie zeigten sich an den Neugeborenen interessiert, halfen aber bei der Geburt nicht mit. Drei Jungtiere wurden in Scheitellage, zwei von ihnen in occiput posterior, eines in occiput anterior geboren. Der letztgeborene Drilling war eine Steißgeburt. Die Mutter und die übrigen Familienmitglieder kümmerten sich nicht um ihn. Bis auf den letztgeborenen Drilling klammerten sich alle Neonaten sofort nach ihrer Austreibung am Fell der Mutter fest und krabbelten selbständig zu deren Zitzen. Ein ♀ fraß die Plazenta einschließlich des Nabelstranges selbst auf. Dem anderen ♀ wurde die Nachgeburt von Gruppenmitgliedern entrissen und verzehrt.

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The anatomy of the eye of the Ganges River Dolphin
Platanista gangetica (Roxburgh, 1801)

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Introduction

In the scientific and popular literature about vision or about cetaceans, the "blind" River Dolphin is a favourite subject, being frequently mentioned as the only known aquatic mammal with degenerate eyes. In contrast with this popularity, descriptions of the anatomy of the eyes (or their rudiments) are extremely scarce. Apart from Pliny the Elder, who — according to Herald and co-workers (1969) — had already written about the species, the first description was offered by Roxburgh in 1801 in a publication which is difficult nowadays to obtain (Pilleri 1971). As cited by Eschricht (1851), Roxburgh limited his remarks on the visual organ to one sentence: "Eyes exceedingly minute, being only a line in diameter and sunk pretty deep in their small round orbits". Cuvier (1836) gave much the same comment, with the sole addition that the eye colour is black. The note made by the Danish zoologist Reinhardt at the examination of a fresh animal in Calcutta during the Galathea-expedition in 1845, which is reported by Eschricht (1851), gives no more information: „Öiet var overordentlig lille; dets diameter kun 1¹/₂'''.". The skeleton of this same animal was examined by Eschricht, who concluded from the rudimentary character of the optic foramen that the dolphin must be blind.

A great contribution to the knowledge of the *Platanista* eye was produced by Anderson (1878), whose report remained the only more detailed one for nearly a century. The author summarizes (p. 470): ". . . the rudimentary nature of the eye — rudimentary in the absence of a crystalline lens; . . .; the glandular and tactile character of the conjunctival investment of the cornea; and the very feeble optic nerve; all lead to the conclusion that this mammalian eye can be of little more use than as a feeble receiver of impressions of light.". Though with hesitation, he does not exclude the existance of visual power of some kind in this species.

In a paper on the central nervous system of whales by Pilleri and Gihr (1969), a few data are given on the dimensions of the eye bulbus and the optic nerve of *Platanista*. In the study of *Platanista,* made by Herald c. s. (1969), the eye was not the main subject; nevertheless, their brief anatomical description contains substantially new information with regard to the retina, on which they base their opinion that some vision, useful to the animal in some way, is not beyond the possibility of the visual organ.

The total available information on the subject, gained in nearly two centuries, has been summarized in the above few paragraphs. That the information is far from complete may be illustrated by the fact that, based on the anatomy, both Anderson and Herald c. s. considered some visual power possible in *Platanista,* while neither observed any behaviour in favour of vision in living animals. It seems that additional information about the eyes and vision in this remarkable mammal is greatly needed.

Material and methods

By courtesy of Prof. M. Nɪsʜɪwᴀᴋɪ, University of Tokyo, Japan, we received the eyes of a female *Platanista gangetica,* registered under nr. 16 in the University's collection. The animal, measuring 120.5 cm in body length, had been captured north of Tistamukh Ghat of Kola River, Bangla Desh, and transported alive to Japan. It was a juvenile specimen, the age of which was estimated to be between one and two years old.

After the animal died in april 1970 the eyes, together with the lids and surrounding tissues were taken out and preserved in Zenker's fluid. We received the material, accurately bisected axially, in the preserving fluid (Fig. 1).
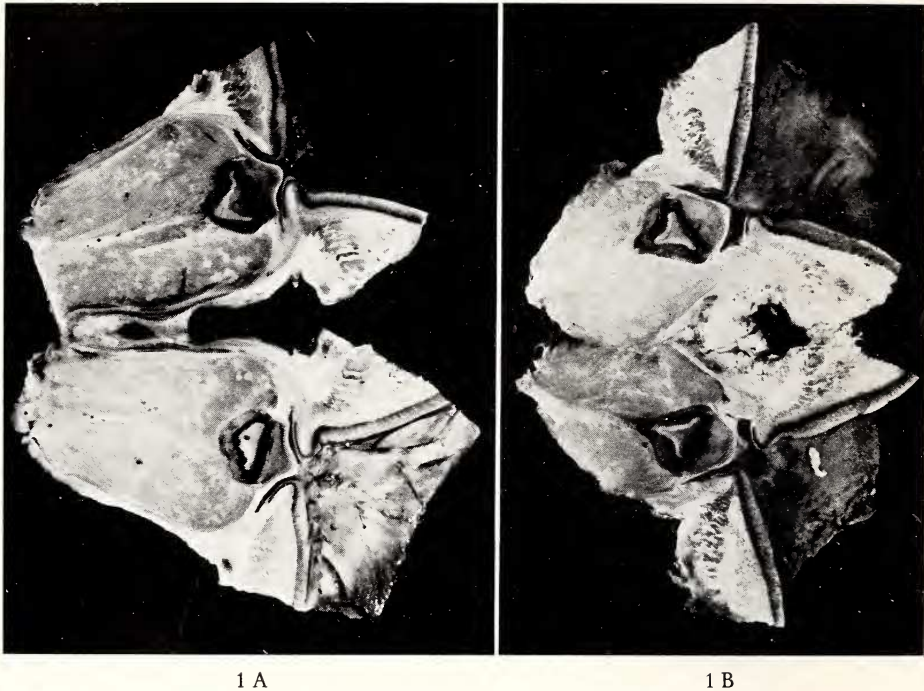

1 A   1 B

Fig. 1. Platanista gangetica. The bisected eyes before embedding

By putting the adjacent halves together, we could observe the shape of the lid-opening and compare it with that given by Aɴᴅᴇʀsoɴ (1878) in his figure 17A (p. 468). It appeared that one of the eyes had been bisected in a horizontal plane (i. e. parallel to the body axis) and the other one in a vertical plane. In the latter, the eccentric position of the pupil and the optic nerve enabled us to decide on the dorsal and ventral sides. In subsequent microscopic examination this decision was confirmed by the distribution of the pigment in the retinal epithelium. If the lid-opening of *Platanista,* however small this may be, bears any resemblance with that of other odontocete species, the vertically bisected eye must have been the right one; the conclusion remains doubtful, however. We found no clues in the horizontally cut eye to allow determination of the nasal or temporal sides.

After the normal procedure to remove precipitates of preservative the eyes were embedded in nitrocellulose, following the technique described by Bᴇᴜᴍᴇʀ (1963). Sections of ca. 20 microns were cut and stained with H. E., P. A. S. and Azan.

In addition to those of *Platanista* we made similar observations on eyes of other odontocete species and in our opinion the eye of *Tursiops truncatus* makes a suitable standard for comparison. The results have been published for only a small part until now (Dʀᴀʟ 1972), but anticipating further publication we have compared in a few instances the eye of *Platanista* with that of *Tursiops* in this paper.

Gross anatomy of the eye and its adnexa

It is clear, even from the relatively small pieces of tissue which we had at hand, that the eyes were situated very deeply in the head of the animal. The surrounding skin formed a cone with an apex angle of about 90° (Fig. 1, 2); no separate lower and upper eyelids were definable. The lid-opening of the horizontally cut eye had a nearly regular oval outline, but in the other eye it was egg-shaped. The dimensions were respectively 1.7×0.9 and 1.45×0.9 mm, the longer axis lying horizontally. The dimensions of the opening can doubtless be changed by the strong sphincter, surrounding it (Fig. 2, sm), and by a less powerful muscle having a hollow, cylindrical shape (Fig. 2, cm), which stretched from the sphincter in a posterior direction. The cylindrical muscle has been cut at the posterior side in our preparations; according to HERALD c. s. (1969) it had been attached to the orbit. Between the muscle and the eye bulbus, and with branches into the eyelids in places, was a ring-shaped gland (Fig. 2, gl), which apparently emptied its secretion by a number of tubes into the spacious conjunctival sac. The space in the muscular cylinder was filled with adipose tissue, which embedded the posterior side of the eye bulbus.

The size of the eye bulbus could not be estimated accurately in our material; however, its external diameter in horizontal as well as vertical direction would be approximately between 4.0 and 4.5 mm. PILLERI and GIHR (1969) mention data of 4.2 and 5.0 mm for the horizontal and vertical diameter respectively. That the latter dimension is the larger one contrasts markedly with the relationship usually found in
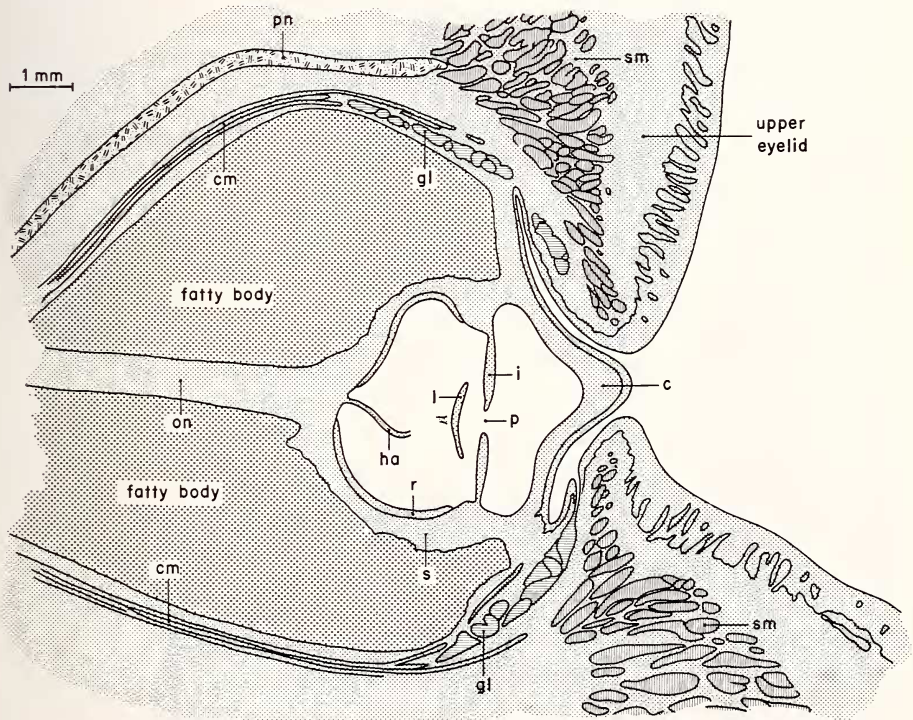

Fig. 2. *P. gangetica.* Schematic vertical cross section through the eye. pn = peripheral nerve; sm = sphincter muscle; cm = cylindrical muscle; gl = Harder's gland; on = optic nerve; ha = hyaloid artery; l = lens; i = iris; p = pupil; c = cornea; r = retina; s = sclera

odontocetes (PÜTTER 1903; ROCHON-DUVIGNEAUD 1943; a. o.). Even more unusual is the fact that the axial diameter of the *Platanista* eye, being about 5.5 mm according to our measurements, was the largest of the three — at least certainly not smaller than the other two. This was due to the strong forward curvature of the cornea (Fig 2, c), which produced an exceptionally wide anterior eye-chamber.

Perhaps we were dealing with an artifact, caused by strong contraction of the sphincter in the eye-lids and the cornea ought to have been flat, in accordance with the description by HERALD c. s. (1969). In that case, however, one should have expected the iris to be distorted in our preparations also but this expectation was not fulfilled.

The eyelids covered the cornea for a substantial area, especially on the dorsal side. As was the case with the bulbus, the diameter of the cornea could only be measured approximately; along a straight line from limbus to limbus it was approximately 3.5 mm. The cornea was thicker at the apex than at the periphery, unlike the relationship in other odontocetes, where as a rule the opposite is the case. Also remarkable was the thickness of the bulbar part of the conjunctiva, and the free course it took after leaving the limbus.

The sclera was thin and there were no extra-ocular muscles attached to it. The "eyeshine", which is usually seen in cetacean eyes — including in preserved material — and which indicates the presence of a tapetum lucidum, was absent in *Platanista*. The choroidea was inconspicuous because it was poorly provided with pigment. The anterior surface of the iris was shiny and flat, the posterior side being clearly ribbed by the processi ciliares. The colour was dark brown; nevertheless the pigmentation was not very dense and light was not entirely prevented from passing through the iridial tissues (Fig. 3). The pupillary aperture was less than half a mm in diameter. In vertical section it was situated somewhat ventrally from the centre, which suggested the existence of an operculum.

The optic nerve, in its silvery, shining sheath, left the bulbus somewhat dorsally of the posterior pole and took a slightly waving course through the fatty body. Including its sheath the diameter was 0.7—0.8 mm.

Microscopic anatomy

1. Adnexa

Eyelids

The skin of the exposed side of the eyelids was covered by an epithelium with a minimum thickness of 200—250 microns. If measured including the papillae, however, it was up to 1000 microns. Towards the lid-opening the depth of the papillae decreased. The most superficial layer of about 30 microns thick contained no nuclei and was cornified. A layer of fusiform cells of about equal thickness, adjacent to it, showed a tendency to stain differently from the deeper cell layers, which morphologically formed a gradual transition to the highly cylindrical basal cells. The longer axes of

Fig. 3 — Fig. 6 See opposite page

Fig. 3 (above left). *P. gangetica*. Photomicrograph of the iris with transmitted light. Toto, unstained — *Fig. 4 (above right)*. *P. gangetica*. The epithelium of the palpebral conjunctiva. In the epidermis a nerve glomerulus. H. E. stained — *Fig. 5 (below left)*. *P. gangetica*. A few bundles of the sphincter of the eyelids (A) and a part of a peripheral nerve (B.) Van Gieson stained — *Fig. 6 (below right)*. *P. gangetica*. Cylindrically shaped muscle near the posterior border of Harder's gland, where cross striated and smooth muscle fibres appear together. Azan stained
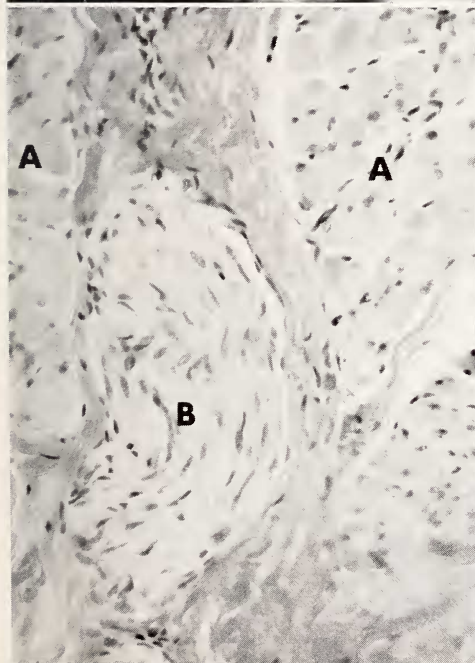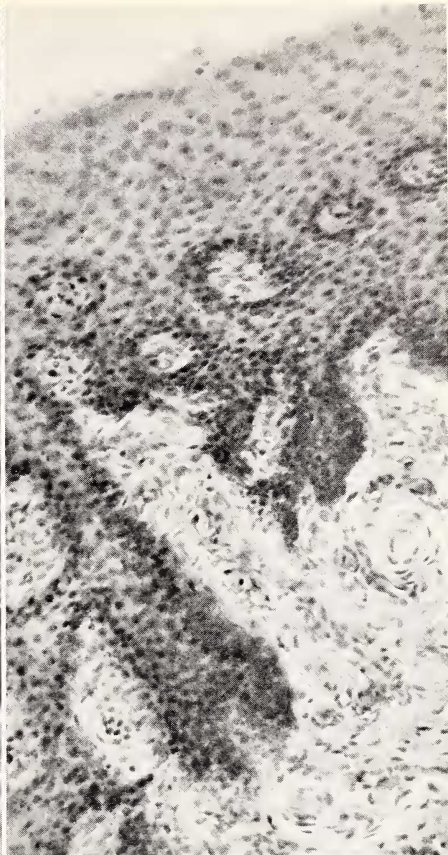
the basal cells were directed to the outer surface of the skin, which made them lie at acute angles to the papillary borders. In the papillae the flatter cell layers were stratified perpendicular to the outer surface of the skin, passing arcuate round the interpapillary ridges and thus merging with the stratification parallel to the skin surface predominant in these regions.

The nuclei of the basal cells were almost circular with a diameter of 7—10 microns; more superficially they took on an oval shape. All nuclei carried distinct nucleoli and many had a cap of pigment granules on the outward side. As the nuclei were most closely packed at the deepest parts of the papillae, most pigment was found in these regions.

A basement membrane, if present at all, was indistinct.

Many nerve glomeruli were present in the papillary layer of the epidermis and especially in the epidermal ridges at the outer side of the eyelids; such nerve endings were present also in the derma of the palpebral conjunctiva, though perhaps less abundant (Fig. 4).

The subcutaneous layers of resp. the outer skin and the conjunctival derma were united to a continuous body of connective tissue, provided with many capillaries and incorporating the orbicular muscle. There was, contrary to the condition found by ANDERSON, no fatty tissue in the eyelids.

Conjunctiva

The epithelium of the outer skin of the eyelids continued around the margin of the lid-opening as the conjunctival epithelium. Along this course there was a gradual but rapid morphological transition. The papillae became shallower and the cornified layer disappeared. For both reasons the total thickness of the epithelium decreased. In the first part there were only a few layers of cuboidal basal cells, covered by several layers of squamous cells, the most superficial one being thinnest. Unlike the skin, pigment was restricted to the basal cell layers, which were richly provided with brownish granules. Near the fornix the basal cells suddenly became highly columnar, the superficial layers less squamous and even cuboidal here and there. The thickness of the epithelium remained unaltered, as the number of cell layers decreased to some 4 or 5 in this region. Between these cells several unicellular mucous glands could be observed. Pigment granules were present all over in this region, the higher concentrations being near the free surface, where dense clusters could be found. Scattered melanocytes occurred in the subepithelial dermis here.

On the bulbar conjunctiva, between fornix and limbus, the epithelium reached its minimum thickness (not including the few and small papillae) of about 50 microns. The basal cells were cuboid or shallowly cylindric and covered by a number of layers of flattened cells. Only the most superficial layer was squamous; there was no cornification.

The stroma of the conjunctiva was a continuation of the connective tissue of the eyelids and continued into the cornea, the sclera, and into the other adjacent tissues.

Even more so than in other parts, the stroma of the bulbar conjunctiva was richly provided with blood capillaries. It is a remarkable feature that this part did not overly the eye bulbus; instead it formed the anterior border of the fatty body around the bulbus. On the other hand, cne might consider the fatty body as a part of the sclera, which would normalize the position of the bulbar conjunctiva, but would provide *Platanista* with a sclera of unique composition.

Musculature

The powerful sphincter, present in the eyelids, consisted of a great number of bundles of cross-striated fibres (Fig. 5, A), embedded in connective tissue. The inner border of the muscular ring, formed by bundles of a smaller diameter, lay closely under the epithelium of the rim of the eyelids (Fig. 2), the outer border of the muscle being lacking in our preparations.

The cylindrically shaped muscle, surrounding the fatty body and isolated from this by a layer of connective tissue, was comprised of several layers of striated muscle tissue, alternating with layers of collagenous tissue. The muscular fibre bundles were orientated mainly antero-posteriorly, but a minority followed a slightly oblique course. On meeting the posterior side of Harder's gland the muscle split, sending a few fine branches along the inner side of the gland and a greater number along the outer side (Fig. 7). The latter, diminishing rapidly in size, could be traced up to very near the sphincter muscle. Meanwhile a transition from striated to smooth muscle tissue had taken place. In part, this happened shortly posteriorly to the point of splitting, in which region the cross striation disappeared in a number of fibres, giving the tissue the appearance of smooth muscle tissue. The branches at the inner side of the gland were entirely built up of smooth muscle cells, at the outer side of the gland, however, a mixture of striated and smooth cells remained visible (Fig. 6); more anteriorly the muscle continued in small bundles of smooth cells only. Its position as well as its dual structure suggests that the cylindrical muscle represented the levator muscle of the palpebrae, in which case its smooth part represented Müller's muscle. The latter, at least in human eyelids, is a (smooth) muscle connecting the (striated) levator muscle to the tarsal plate.

Nerves

The — presumably tactile — nervous elements, present in the skin and conjunctiva, have already been mentioned above. Several relatively coarse peripheral nerves could be found in the connective tissue surrounding the cylindrical muscle. At least one of them found connection with the palpebral sphincter (Fig. 5 and 7) at a place somewhat dorsally to lateral. It had a diameter of ca. 100 microns and contained many myelinated fascicles of 5—15 microns thick.

Harder's gland

At the position described before (Fig. 2, gl) there was a ring-shaped acino-tubular gland. In order to conform with the relevant literature, we prefer to identify it as Harder's gland, though neither its position, nor its structure justifies this choice.

The gland was made up of a great number of lobules of very varying sizes (Fig. 7). The glandular cells were columnar to cuboidal, with the nuclei situated basally. The basal plasma reacted basophilic, but apically it stained less densily. Several ducts connected the gland with the conjunctival sac, some being at the fornix, others more at the palpebral side. The ducts had a cuboidal epithelium, becoming squamous near the end in continuation with the conjunctival epithelium.

Fatty body

The fatty body consisted of the normal adipose tissue and shows in our sections the common "ring cells". Its collagenous fibres were continuous with those of the connective tissues which surrounded or were enclosed by it.
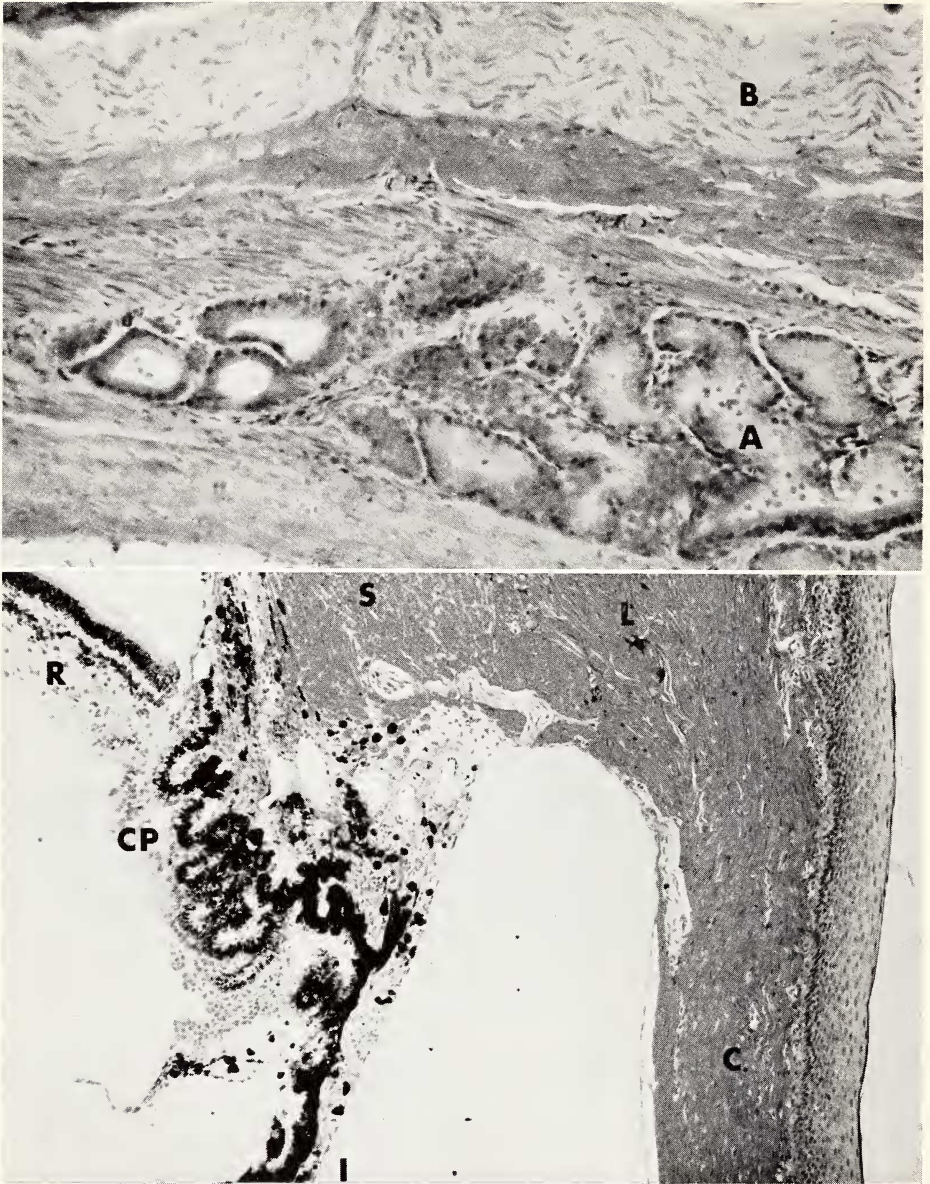
Fig. 7 (above). *P. gangetica.* Part of harder's gland (A), on the outer side and part of the inner side lined by muscular tissue, and the peripheral nerve (B) connected with the palpebral sphincter. H. E. stained — *Fig. 8 (below). P. gangetica.* Dorsal side of the iris angle. Azan stained. C = cornea; L = limbus; S = sclera; R = retina; CP = ciliary processes; I = iris

2. The optic vesicle

Cornea

The corneal epithelium had a thickness of about 125 microns at the apex, gradually decreasing to some 80 microns peripherally. Structurely it resembled the conjunctival

epithelium, including the indistinctness of a basal membrane. Though there were no true papillae, the epithelial basis was not as straight as we had observed in the cornea of other species of cetacea. It followed a wavy course, disrupted now and again by epithelial cysts, which may have been scars of former superficial injuries (BEUMER c. s. 1972). Anteriorly there were only one or two layers of squamous cells. There was definitely no cornification. Slight indications of cornification (Fig. 8) were interpreted by us as artifacts, caused by maceration.

Bowman's membrane was absent, unless it was represented by a very narrow band, adjacent to the epithelial basis, which in some cases stained somewhat less intensively than the rest of the corneal stroma.

The stroma centrally measured about 350 microns, down to about 240 microns peripherally. This connective tissue was rich in cells; many nuclei had nucleoli. The lamellar construction of the stroma could be recognized, though the alternating organization of the fibrils is not nearly as regular in this eye as is the rule in most mammals and as we have encountered in *Tursiops truncatus*.

Blood capillaries were present throughout the corneal stroma, an exceptional feature in the healthy mammalian eye. As we did not see any additional indication that our material was anomalous, we were inclined to believe that the presence of capillaries in the cornea is normal in *Platanista*.

A very thin membrane of Descement could be discerned after P.A.S.-staining. The endothelium was well developed. It covered the posterior surface of the cornea apparently without gaps and continued over the filtration angle and the anterior surface of the iris.

Limbus

The limbus is a definite transitional zone between cornea and sclera in other odontocete species, but was rather undefined in *Platanista*. This was mainly due to the fact that the fibrils in this region, as well as in the regions on either side of it, were much less regularly orientated as is the case in the other species. In the limbus of *Platanista* the collagenous fibres coursed in all directions, without pattern, except for a bundle of circularly disposed fibres at the scleral side. In this region some chromatophores were present, but few in number again in comparison with other species (Fig. 8).

The limbal epithelium thickened gradually towards the cornea, being continuous with the corneal and the conjunctival epithelium on either side.

The presence of many capillaries in the bulbar conjunctiva as well as in the corneal stroma was due to the fact that the superficial marginal plexus occupied an area with no apparent boundaries. This plexus, however, could be recognized in individual sections in a series by the slightly coarser appearance of its vessels and by the fact that these vessels were connected with the filtration angle.

Sclera

Though, as said above, the fatty body may also be part of the sclera, only the collagenous part is described here. The thickness of this part was about 150—200 microns and did not show the increase in thickness towards the posterior pole which is commonly met with in cetacean eyes. The collagen fibres were wavy and arranged in layers in which the fibres ran roughly in two directions: antero-posteriorly and circularly. The antero-posterior direction was mainly followed by fibres at the inner side of the scleral cup; circularly running fibres were mainly concentrated in the outer layers. Radially running fibres, as described by PILLERI c. s. (1964) in *Balaenoptera*

and as observed by us in *Tursiops,* were not present in *Platanista.*

Melanophores were scattered throughout the scleral tissue, nowhere very numerous, but in greater numbers near the choroid, around the few bloodvessels and near the optic nerve sheath.

Loose episcleral tissue was lacking; the scleral fibres were directly continuous with those of the surrounding adipose tissue.

Choroidea

Though the total thickness of the choroidea nearly equalled that of the sclera, it was poorly developed in comparison with that of *Tursiops.* When compared with the (much bigger) human eye, however, the thickness and vascularisation of the vascular layer of the *Platanista* eye was not inferior. Scattered throughout the choroid were a few melanophores, which, in turn, carried a few pigment granules.

Supra-choroidal lamellae were present in small numbers at some places. More often the scleral tissue changed abruptly into loose connective tissue, filling the spaces in the vascular layer. The latter consisted of rather coarse vessels, compressed parallel to the retinal plane and arranged in one or, more rarely, two layers. The loose connective fibres between the vessels were redistributed into poorly oriented lamellae at the retinal side of the vascular layer to form a thin (max. 45 microns) and poorly organized tapetum. This tissue was perforated at intervals by capillaries, supplying a well developed chorio-capillaris.

It is perhaps unlikely that Bruch's membrane was absent, but we could find no trace of it.

Ciliary body

The differentiation of the ciliary body from the choroid could be considered to start at a short distance posteriorly of the ora serrata. From here the choroidal vessels became progressively wider (Fig. 8 and 9), while the supra-choroidal lamellae, as far as they were present, became lost by continuing in the abundance of connective fibres between the vessels. Anteriorly the ciliary body merged into the tissues of the iris and filtration angle. The whole structure stood out as a protrusion of the sclera, characterized by the more numerous and much more densely pigmented melanophores than were present in the adjacent tissues.

Immediately adjacent to the ora serrata the body carried ciliary processes, which were hardly less developed than in the much larger eye of *Tursiops.* As usual, these processes were covered by the two cell layers of the ciliary portion of the retina. They were of the primitive, rugose and puffy type and continued on the posterior side of the dorsal iris segment, where they were much more slender (Fig. 13).

Iris

The iris was thin, with a minimal cross section at the root of the ventral and lateral quadrants of 50 microns and 60 microns dorsally. The maximum thickness amounted to 100 microns ventrally and 125 microns dorsally. These maximum sizes were due to the presence of the smooth muscular system, especially the sphincter, which, regarding the dimensions of the iris, could be considered to be reasonably well developed (Fig. 10 and 12). A dilator was also present, but without depigmentation its extension remains obscure. The strictly radial direction in which the inner cells of the iridial portion of the retina were orientated, makes us suppose that the dilator stretched from near the pupillary margin to not far from the root of the iris (Fig. 9), dorsally

Fig. 9. P. gangetica. Ventral side of the iris angle. P.A.S. stained

Fig. 10. P. gangetica. Central part of the iris and the lens from the horizontal section sketched in Fig. 11 a. H. E. stained

even further (Fig. 8). This cell layer contained much pigment; the adjacent cell layer, covering the iris posteriorly, was free of pigment or, in the dorsal quadrant, nearly so.

Anteriorly the iris was covered by an endothelium, seemingly an uninterrupted continuation of the corneal endothelium. The stroma contained occasionally some melanocytes, most of them being fully contracted and a few branched. These cells were much less abundant than is the case in the *Tursiops* iris; moreover in *Platanista*

the individual cells were less densely pigmented. Embedded in the loosely woven stromal tissue were relatively few and small sized blood vessels. These did not "bridge" freely in the anterior chamber as has been described in a number of species (ROCHON-DUVIGNEAUD 1940) and as is the case in *Tursiops*. In *Platanista* the anterior surface of the iris was perfectly flat. Because the stromal vessels were present up to immediately against the endothelium, a vessel-free anterior sheet was lacking.

Filtration angle

In contrast with other cetacean species the angle of the anterior eye chamber had the shape of a wide bay (Fig. 8). At the posterior side a coarse spongium iridocornealis was present. The over- lying endothelium showed perforations in this region. We are not sure, however, whether these were artifacts or not. The spongium consisted of coarse, circularly directed collagen fibres, the spaces between being frequently traversed by a reticulum of finer fibrils. At places, especially at the lateral quadrants, the trabecular system was hardly differentiated. In the ventral (Fig. 9), and even more so in the dorsal quadrants (Fig. 8), the spaces were very wide and conspicuous. If the endothelium was indeed perforated, these spaces were continuous with the anterior eye chamber on one side; at the other side they were connected with small vessels, which in serial sections could be followed to the superficial marginal plexus. Coarser vessels running in the vicinity of the spongium belonged to the vascular portion of the ciliary body and were continuous with the choroid.

Peripheral nerves could be observed in and around the trabecular system, extending in the limbus and periphery of the cornea (Fig. 8). At these places we never found any nervous tissue in *Tursiops*. It was especially abundant in the dorsal part, much less ventrally and absent in the lateral quadrants. The position of these nerves in or near the spongium irido-cornealis was reminiscent of

Fig. 11. *P. gangetica.* Sketches of a horizontal (a) and a vertical (b) section of the iris and lens. The horizontal section passed some- what dorsally of the eye-axis, the vertical section is close to axial.

the sensory corpuscles, described by ROCHON-DUVIGNEAUD (1940) and PILLERI c.s. (1964). Structurely, however, there was no resemblance to these corpuscles.

Lens

The lens, hitherto considered to be absent in this species, had only a few character- istics in common with the mammalian type, and even less with the typical cetacean eye lens. Its form resembled that of a watch-glass with a central thickening, the concave side being towards the iris (Fig. 11). The iris should perhaps be flat in the horizontal section represented by Fig. 11a. Its curvature is probably a result of preparatory technique. The lens should also be less curved and its shape more in correspondance with that in Fig. 11b. Doubtless there are some dislocations, due to

preparatory technique, in the vertical section (Fig. 11b). The lens was perhaps displaced in a vertical direction or, even more probably, the dorsal part of the iris and connected tissues were displaced dorsally. Nevertheless a view on both sections gives an idea about the shape and interrelationships of the structures in this region of the eye.

The lens had a diameter of 1.5 mm; the maximal axial size being about 140 microns.

Unlike the situation in mammalian eyes, the capsule was not the outer-limiting structure of the lens. On its anterior side the capsule was covered by a layer of very flat cells (Fig. 10, 13, 15 and 16), carrying fine capillaries at a few places (Fig. 15

Fig. 12 (above). P. gangetica. Vertical section, showing the dorsal part of the iris with sphincter and the rim of the lens with a cellular extension in connection with a zonular fibre. A similar cellular structure is seen between iris and ciliary processes. H. E. stained. — *Fig. 13 (below). P. gangetica.* Vertical section, showing the dorsal part of the iris and bicellular extensions from the ciliary processes and from the lens equator. Azan stained
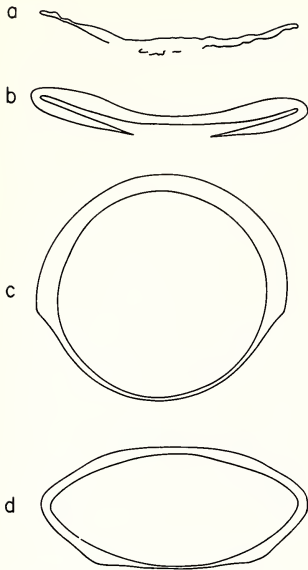
Fig. 14. Comparison of the lens capsules of different species. a: capsulum of *Platanista* as present in the vertically sectioned eye; b: the same, schematic and in thickness 5 times oversized; c: capsulum of *Tursiops,* schematic and in thickness 10 times oversized; d: capsulum of *Homo,* schematic and in thickness 20 times oversized (after DUKE-ELDER, modified)

and 16). Though our material was too limited to be conclusive, this cell layer seemed to be continuous all over the anterior lens surface (Fig. 13). This latter fact was true at least for the dorsal side of the lens; with respect to the ventral and lateral sides, however, we are less certain. It was also only on the dorsal side that the anterior and posterior layers formed a bicellular extension, which in certain cases (Fig. 12) could be seen to be continuous with zonula fibres. On the other hand, however, similar bicellular structures were present in the neighbourhood of (Fig. 12) or connected with (Fig. 13) the ciliary processes and it is by no means impossible that the lens and the ciliary processes were directly interconnected by these cellular structures. The fact that chromatophores could occur in the lenticular extension (Fig. 13) makes this suggestion the more plausible. Unfortunately the section which would have shown conclusively the connecting part of both bicellular structures in Fig. 13 was lacking in our collection. Doubtless the situation was complex generally, but more material should be available to gain a clear picture.

In the central parts of the posterior lens surface the capsule — as far as present — was also covered by cellular tissue (Fig. 15). This however had the character of connective tissue and was interpreted as part of the hyaloid artery.

The capsule could be recognized by its structure — or rather lack of structure — and its staining reactions. It was continuous over the anterior lens surface and around its equator, tapering off on the posterior side and becoming indistinct in the posterior central area (Fig. 14a). In this area, some chaotic fragments of the capsule were present in the lens of the vertically sektioned eye; in the other lens, even these fragments were absent. In relation to the size of the lens, the capsule was thick as compared with that of Man. The same is the case in *Tursiops* and probably other cetaceans. (Table and Fig. 14. Note that in this figure the magnification of the capsule thickness in b is x 5, in c x 10 and d x 20!) The wringled appearance of the capsule of the *Platanista* lens (Fig. 14a), together with the fact that it carries more or less globular thickenings here and there (Fig. 15) and steep thinner places on the posterior side, makes the determination of its thickness difficult. However, comparison between a number of sections, horizontal and vertical, provides some reasonable approximations (see Table).

In the *Platanista,* the capsule of the lens had a thickness approximately equal at the anterior pole and at its equator, while between these points it increased to about twice that value. At the posterior side of the lens the thickest parts were found near its equator. These relationships are reminiscent of those in the human eye rather than of those in odontocetes. Since we may take it for certain that the *Platanista* lens is non-accommodative, the morphological similarity cannot indicate a similar function.

The subcapsular epithelium formed a distinct unicellular layer at a few places only (Fig. 16). The cells were roughly cuboidal at these places, with round or

Table

Thickness of the lens capsule in microns

The data for *Homo* are dirived from Duke-Elder (1961, Vol. II, p. 314). The data for *Platanista* are approximations

Species	lens ⌀ in mm	ant. pole	ant. max.	equator	post. max.	post. pole
Homo, 35 years old	9.0	14	21	17	23	4
Plantanista gangetica	1.5	10	20	10	10	0
Tursiops truncatus at corresp. places	9.0	54—57	ca. 66	76—79	10	12—13

oval nuclei. At the thinner parts of the lens the epithelial cells had a more flattened shape and the nuclei shaped accordingly. The nuclei were characterized by fine and regularly distributed chromatin and by the distinct nucleolus. At places where the capsule showed extensions into the lenticular body (Fig. 15), the epithelial cell layer was either interrupted or displaced and folded into a multicellular structure.

The initiation of the formation of crystalline fibres could be found here and there at the nuclear zone (Fig. 16). At infrequent places the epithelial cells were elongated and oriented in the usual way. This limited state of differentiation seems never to be exceeded; we did not find a single fibre with disappearing nucleus.

This implied that the lens of *Platanista* lacked a crystalline body. The space which it should have occupied — and which in this thin lens was only available in the central part — was largely filled by the above-mentioned capsular protrusions and the irregulary folded epithelium. Apart from these there were some vacuolelike amorph and sometimes quite extensive structures (Fig. 10 and 16), the nature of which we could not determine.

Zonula Zinnii

A few remarks on the zonula have been made above already. In *Platanista* as many zonular fibres as in other mammals ran without crossing from the angles between the ciliary processes to the lens. They were attached to the latter in a ring-shaped zone from its equator (Fig. 12) for some 400—500 microns centrally on the posterior side of the lens (Fig. 9 and 16).

Vitreous body

The vitreous body presented the usual picture of a reticular coagulate. The body was traversed by a hyaloid artery, following an undulating course from the optic papilla (Fig. 17) to — presumably — the posterior surface of the lens. We could not be sure about this, because some sections were missing and only the parts sketched in Fig. 2 were represented. These blood-filled regions showed no sign of degeneration.
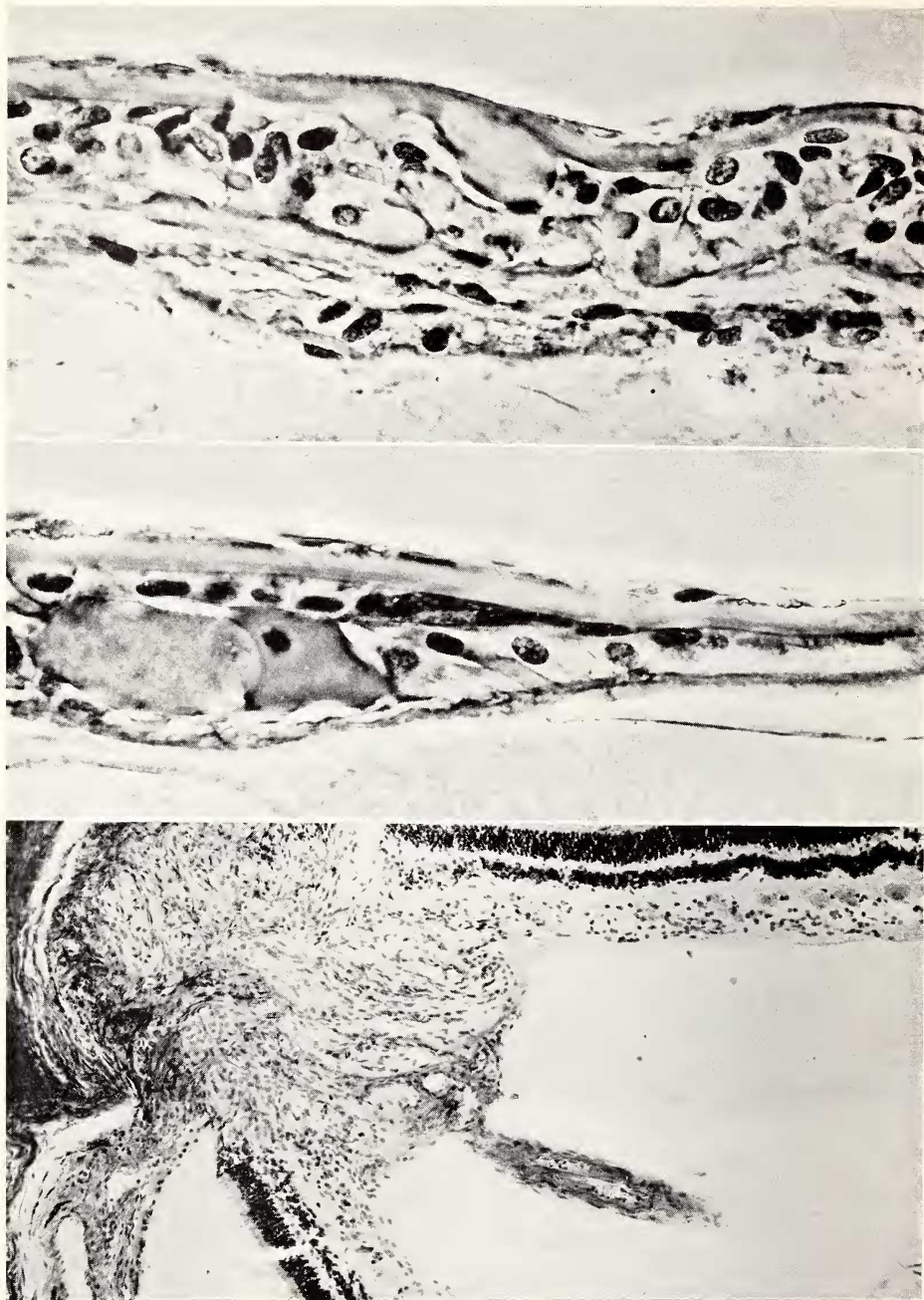
Fig. 15 (above). P. gangetica. Vertical section of the lens, showing capsular protusions, folded epithelium and posteriorly adhering connective tissue. Azan stained, phase contrast. — Fig. 16 (centre). P. gangetica. Vertical section of the lens, showing a regularly arranged epithelium and the transition to crystalline fibres. Azan stained, phase contrast. — Fig. 17 (below). P. gangetica. Optic disc with part of the hyaloid artery. Azan stained

Retina

The extreme shrinkage of the vitreous body had detached the retina from its epithelium and only near the ora (Fig. 8 and 9) and papilla (Fig. 17) did it remain at its original place. This is why the retina has been cut at different angles in various parts of the sections, making measurements of the thickness of the retinal layers very unreliable. Another obstacle to measurement lay in the fact that the layers, though clearly defined when regarded at low magnification, appeared to be rather diffusely bordered at higher magnifications (Fig. 18). By measuring and counting in a variety of sections at those places where the retina was thinnest and thus cut closest to perpendicular to the surface, we hoped to achieve at least acceptable approximations.

The overall thickness of the retina was about 250 microns, being only slightly less near the ora serrata (Fig. 9). Capillaries traversed the retina in all directions, fine ramifications penetrating as deep as the outer plexiform layer.

The pigment epithelium consisted of one layer of cuboidal cells, 6—8 microns high and 10—15 microns in width. The flattened, disc-shaped nuclei had a diameter of 7—10 microns and measured 3—5 microns radially. Though nowhere completely absent, pigment granules were very sparse. Only in the peripheral parts, especially on the ventral side, was the pigmentation more dense. Such a distribution of the pigment conforms with that usually found in eyes with a tapetum lucidum.

The thickness of the bacillary layer (Fig. 18, 2) may have been some 30 microns. Autolysis left little detail in the photo-sensitive elements. In connection with the structure of the nuclei, to be described below, it may be worth while to mention that many receptors showed swollen tips, which is, according to MAXIMOW and BLOOM (1957), an autolytic artifact, characteristic for cones.

The outer limiting membrane (Fig. 18, 3) stood out clearly, partly because there was a transparent space between this membrane and the nuclei of the adjacent layer.

The thickness of the outer nuclear layer (Fig. 18, 4) was 45—50 microns (including the nucleus-free space of ca. 5 microns along the limiting membrane) in all regions, except for the regions near the ora and around the papilla, where this layer gradually but rapidly thinned out. The nuclei were all of the same type (Fig. 19), round or oval, the longer diameter being 6—8 microns. They were closely packed with their longer axes orientated predominantly radially. Their chromatin was scattered in granules mainly close to the nuclear membrane; one or two larger clumps occupied more central locations. These facts correspond much more with the characteristics of cone cell nuclei than those of rods (Fig. 20).

A row of about six or seven nuclei formed the thickness of the layer. Counted in horizontal as well as in vertical sections, the number of nuclei averaged 12 per 100 microns. This meant that each mm² of the retina contained, roughly, some 85,000—100,000 photo receptive cells.

The outer plexiform layer (Fig. 18, 5), measuring 10—12 microns in width, was divided into two sublayers of equal width, of which the outer stained more intensely than the inner. This was especially noticeable after P.A.S.-staining. In phase contrast illumination the border line between both zones seemed to be built by the bases of roughly triangular structures. The condition of our material did not allow a decision as to whether or not cone pedicles were represented. Nuclei were present scattered through the plexiform layer, being mainly of the types as found in the inner granular layer but more rarely they were cone cell nuclei.

The inner nuclear layer (Fig. 18, 6), 25—30 microns wide, contained nuclei of different types. The most numerous were round or oval nuclei with a diameter of 8—9 microns. Apart from one or two peripherally situated larger clumps, the
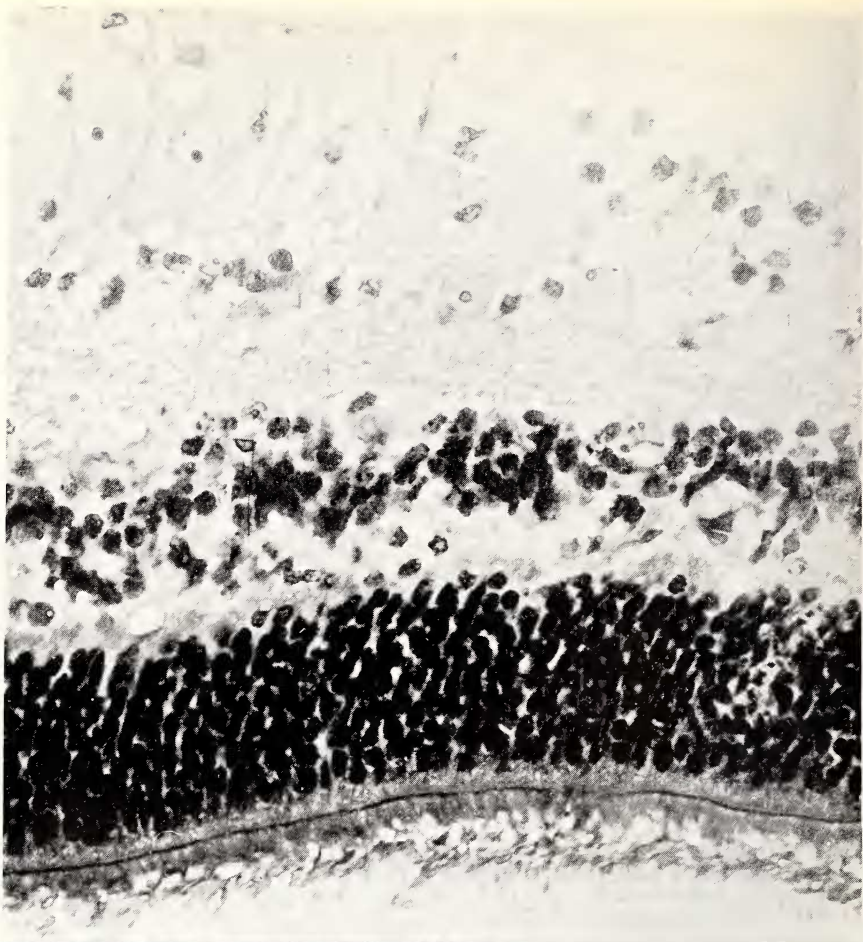
10

8/9

7

6

5

4

3

2

chromatin was dispersed equally through the nuclear body in small granules. Much less abundant, but not uncommon in places, there were oval nuclei, 10—12 microns in diameter, with a nucleolus and pale, finely granulated chromatin. An empty space around these nuclei indicated the presence of a cell body of about 15—18 microns in size. These small ganglion cells were mainly situated at the outer border of the inner nuclear layer. Nuclei of different structure were also present, including large ganglion cells, which characteristically belonged to the ganglion cell layer. Because, however, fixation and staining were not specific, an identification of the cell types was not possible.

The inner plexiform layer (Fig. 18, 7) was represented by a reticulum without detail, owing

SPECIES	CONE CELL NUCLEI	ROD CELL NUCLEI
Homo original		
Balaenoptera physalus after PILLERI and WANDELER,1964		
Delphinapterus leucas after PILLERI, 1964		
Tursiops truncatus original		

Fig. 20. Sketches of the nuclei of cones and rods in man and in some cetaceans.

to bad fixation or autolysis. The width of this layer was 25—30 microns.

As in other cetaceans, the ganglion cell and nerve fibre layers (Fig. 18, 8/9) were intermingled. In this layer there were many roundish nuclei with evenly distributed, moderately coarse chromatin granules and an inconspicuous nucleolus (Fig. 18 and 21). The ganglion cell nuclei were large, up to 20 microns, round to oval, pale with a fine chromatin and a conspicuous nucleolus. The cell bodies, very variable in size and shape, were not infrequently elongated in a radial direction and embedded in fibres of Müller (Fig. 21). The plasma contained a fine tigroid. Patches of these cells were equally spaced all over the retina. In *Tursiops* we found in addition, another type of ganglion cell with a darker nucleus and devoid of a distinct nuclear membrane; this cell type was lacking in *Platanista*. By counting and calculation we arrived at a figure of approximately 850 ganglion cells per mm², so that the total ratio of photo-receptive cells to ganglion cells may have been between 100 and 120:1.

There was a thin inner limiting membrane (Fig. 18, 10).

Fig. 18 (*left above*). *P. gangetica*. Retina. H. E. stained, phase contrast. The layers are numbered traditionally after POLYAK. — Fig. 19 (*left below*). *P. gangetica*. Outer nuclear layer of the retina. Azan stained. Arrow = outer limiting membrane
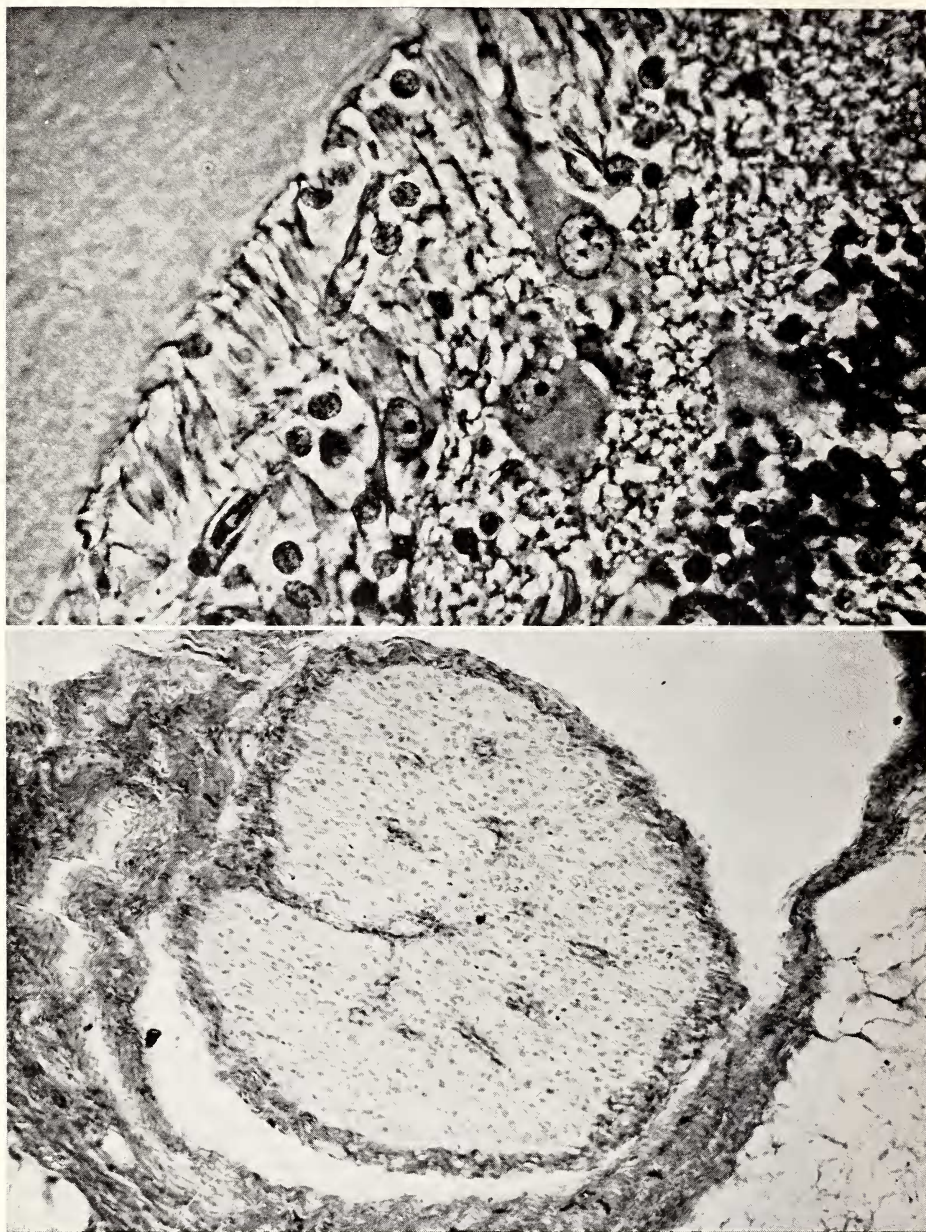
Fig. 21 (above). P. gangetica. Retina, ganglion cell and nerve fibre layers. Azan stained, phase contrast. — *Fig. 22 (below).* P. gangetica. Cross section of the optic nerve. Azan stained

Optic nerve

Wherever it has been mentioned, the nervus opticus has been described as being extremely thin. PILLERI and GIHR (1969), however, demonstrated that its size is normal in relation to the total retinal surface. In vertical and horizontal sections we measured a diameter of 0.50 mm at the optic disc. After leaving the scleral foramen

the nerve thickened gradually for the first part of its length of 1.5 mm, until a diameter of 0.60 mm was reached, after which the diameter remained unaltered.

Though we did not use stains to this end, neural fibrils of various diameters could be discerned. There were certainly more of them than the few hundreds mentioned by Herald c.s. (1969). Neuroglial cells of irregular shape were present in vast numbers.

The nerve trunk was surrounded by the usual three sheaths. The outer one, the dura mater, was the most conspicuous, both by its thickness and the rich content of melanocytes. The fibres of this sheath were continuous with those of the fatty body. On the inner side there was a subdural space, traversed now and again by thin strands of tissue, which connected the dura with the arachnoid sheath. The latter, being the middle one, was only at a few places separated from the inner one by a subarachnoidal space and only at these places was it clearly recognizable as a separate, thin sheath, lined by endothelium on both sides. For the major part, the arachnoid was closely adherant to the pial sheath, which in turn fitted very closely to the nerve trunk. The pial sheath was rich in melanocytes again, especially the parts near the sclera. A pial invagination, carrying some blood vessels, was seen only at a place about 4 mm behind the sclera (Fig. 22); more proximally and distally such coarse invaginations were absent. A few fine pial septa entered the nerve for a short distance, and a true septal system was absent. Instead, several strands of connective tissue ran lengthwise through the nerve, each carrying a capillary with a very narrow lumen (Fig. 22). A few other, thin walled capillaries followed the same course.

The lamina cribrosa was poorly developed. Its presence was indicated only by a few melanocytes, being supported by some connective tissue, which entered the periphery of the nerve near the optic disc.

Discussion

The "degenerate" eye

Ever since *Platanista* was first described, its eye has been indicated as being atrophic or degenerate, which sensuo-stricto means that the eye has been reduced from former excellence to a lower type. One might have expected then, that the eye would have been degenerate in all its parts, including the nervous components, which is clearly not the case in *Platanista*. In our opinion the only structures which can be interpreted as being the results of degeneration are the amorphic vacoules in the eye lens. Other features of the *Platanista* eye, which attract attention by their nonconformity with the typical cetacean eye, are more easily understood if this eye is regarded as being embryonic in structure and not having reached full development. Though not all structures support this view, especially the fact that various parts of the eye seem to have stopped development at different stages, the following features in favour can be emphasized

The presence of a seemingly functional (though not ramified) arteria hyaloidea is a preliminary indication. Even more important, it seems to us, is the covering of the lens capsule by a cellular structure, carrying some capillaries. Most likely, these fine vessels are branches of the hyaloid artery and the structure seems to represent the vascular tunic of the lens. It is true that, regarding the scarcety and extreme small dimensions of the capillaries the tunic of the eye lens of *Platanista* can hardly be called vascular. On the other hand, the proposed point of view finds some support in the fact that in human foetal eyes vessels from the vascular tunic can be seen to be continuous with zonular fibres, resembling the state of affairs which we found in *Platanista* (Fig. 12). With the material at hand we are inclined to interpret the

cellular structure around the lens as representing the vascular tunic, being either not yet fully developed or atrophied to some extend.

Minor indications that the eye of *Platanista* shows embryonic characteristics can be found by comparison with the youngest *Balaenoptera* embryo's, studied by PILLERI and WANDELER (1964), in which the bulbus is globular, the cornea thickest at the apex, the sclera evenly thin and devoid of radially running fibres.

If it be accepted that the *Platanista* eye is embryonic rather than degenerate, some structures might be seen in a new light. The nerves at the iris angle could represent early forms of the sensory corpuscles of ROCHON-DUVIGNEAUD (1940), which are found in some species of cetacea *(Megaptera, Balaenoptera)*, but absent in others (p.e. *Tursiops*). Secondly, the pure cone retina of *Platanista* may be less surprising, at least if there is some truth in the theories (discussed by DUKE-ELDER 1961, p. 252) that cones are transformed into rods during development.

The "blindness" of Platanista

After the present study it is difficult to conclude from the anatomical evidence that *Platanista* is a blind dolphin. Owing to the condition of the retina, the eye must at least be sensitive to light. To perform the act of seeing, however, the formation of an image is required in addition. In aquatic animals the lens is the single effective refracting medium but in *Platanista* the lens, devoid of a crystalline body, can hardly be expected to be optically functional. One might consider stenopaic vision, the pinhole like pupil being the image forming device. Examination of Fig. 2 reveals that, at least with the eyelids closed to this extend, there would be two small apertures behind each other, affecting a form of tube vision. Even if the eyelids could be opened much more, the field of vision would remain very limited, only the central part of the retina, including the blind spot, being operative. The conclusion that *Platanista* cannot use its eyes for true vision seems to be inevitable. Moreover, as far as we know, no behavioural evidence has been reported that the animal examines visually.

It is true of course that a light sensitive retina can be useful — without actual vision — to induce vegetative functions (PILLERI 1970). There are many examples, however, in which such a function is carried out without any retina (many invertebrates, blind fishes etc.), and even in animals with normal functional eyes (MENAKER 1972). So we do not feel satisfied by the idea that this would be the entire function of a retina as well developed as it is in *Platanista*. In this connection the retinal condition may be illustrated by a few calculations.

By reconstruction from the sections we conclude that the diameter of the internal cava of the eye is about 3.2 mm, with a total circumference of 10 mm, of which an expanse of 7 mm is covered by the retina. Measuring along the retina from ora to ora in medial sections we arrive at 5.1 mm, a considerably lower figure, caused by the extreme shrinkage of the retina. Taking this into account, the above mentioned number of ca. 850 retinal ganglion cells per mm² would be $(^{5.1}/_7)^2 \times 850 =$ ca. 400 cells per mm². The retinal surface amounts to about 40 mm², so that the total number of ganglion cells is in the order of 16,000. For reasons of comparison we will calculate the number of nerve fibres per mm² in the optic nerve, assuming that as in man (DUKE-ELDER, Vol. II, p. 234) each ganglion cell in *Platanista* sends its axon to the brain. This would mean that the optic nerve of *Platanista* contains about 16,000 nerve fibres, or, with its cross section of 0.3 mm², about 50,000 fibres per mm². Even if this figure is wrong by a factor of five it still compares well with the 11,700 fibres per mm² in *Phocoena phocoena* (PILLERI and GIHR 1969). In consideration of the small size of the eye in *Platanista,* we must conclude that the nervous part has made the best of a bad job! According to the reasonings of CAIN (1964) the

possession of any structure must be of significance to the animal, regardless whether one can understand its function or not. With the retina of the presumably non-looking *Platanista* we are presented with another structure which is not understood.

The function of vision in cetacea

For reasons given above, visual power of any importance can practically be discounted in Platanista. The lack of vision is commonly ascribed to the muddy water in which this animal lives and in which vision would be of no use. In fact, ANDERSON (1878) proposed this theory, but immediately added the following paragraph (p. 471): "There are difficulties, however, even in such an explanation, because there is not such a wide difference between the conditions of the Gangetic Platanist and those of the Iriwady dolphin, or in anything connected with their respective river-systems as to easily account for the great degradation of the organ of vision in the one case, and the quite ordinarily sized eye in the other, as well developed as that of any marine Cetacean."

On the other hand, one might ask the question the other way around: if *Platanista*, in spite of its lack of vision, is quite capable of surviving, why should other odontocetes need eyes? If *Platanista* can orientate adequately and capture its food by echo-location, the same should hold for marine odontocetes, living in an environment where, however clear it may be, vision is also restricted — at least in relation to their size and speed of movement. It is difficult to imagine circumstances which would attract the visual attention of a dolphin in the ocean and the difficulties met with by trainers in making captive dolphins react on visual stimuli seem to point to the conclusion that vision is unimportant in the normal life of dolphins.

Nevertheless it has been demonstrated (DRAL 1972) that *Tursiops* has eyes which not only see well under water, but also in air, a capability which requires a special accommodative mechanism. Good aerial vision has been found in some other species of odontocetes also *(Delphinapteras leucas, Stenella longirostris, Steno bredanensis;* DRAL, not published) and it may be expected that good aerial as well as aquatic vision will be found to be a general attribute of odontocetes. According to CAIN (loc cit), if an animal possesses such a special capability, it must be of significance.

In summarizing the above paragraph we may conclude that vision in dolphins is unimportant *and* significant, which of course is nonsense. We are inclined to eliminate the contradiction by taking into consideration the cerebral structure of the animals. The complexity of the neocortex has already aroused many uncorroborated speculations and we are about to add another one. There is little doubt that the high cerebralisation endows the animals with special cerebral qualities and it is not beyond the possibility that we have to ascribe to them a consciousness of some level. From psychiatric experience with humans we know that our consciousness is built up and sustained by a constant, great and varied input of sensory impressions. In this respect even information, irrelevant for our biological struggle for life, is indispensable. We venture to suppose that the same holds for the highly cerebrated odontocetes, which for this reason would not give up such an important source of sensory input. It might be coincidence, indeed, but we feel it as a striking fact that the only dolphin with a very poor or even nonexisting vision, *Platanista,* happens to be far the least cerebralized.

Acknowledgements